

The University of Chicago

THE FUNCTION OF THE BRAIN
IN AUDITION

A DISSERTATION SUBMITTED TO THE
GRADUATE FACULTY IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF PSYCHOLOGY

By
L. E. WILEY

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SEVEN TEXT FIGURES AND FIVE PLATES (FORTY-NINE FIGURES)

Experiments on cerebral auditory localization in lower animals have been carried out for the most part upon the dog. The experimenters, on the whole, agree as to the localization of the auditory mechanism, but they disagree as to the manner in which it functions. Munk ('90) concluded that the posterolateral region of the dog's cerebral cortex was auditory in function. He designated this region as B B' B. When only B', which corresponds closely with Brodmann's ('09) area 22, was destroyed, the animal became 'Seelentauben.' It could still hear sounds, but ". . . . er versteht nicht mehr, was er hört; die Bedeutung des 'pst,' 'komm,' und worauf sonst noch er früher eingeübt worden war, ist ihm vollkommen verloren gegangen, so dass nunmehr die Bewegungen ausbleiben, welche er vorher fast maschinenmassig danach vollführte" (p. 30). If, however, there was complete bilateral destruction of area B B' B, the dog was found to be totally and permanently deaf, but his intelligence was otherwise unaffected. The dog was as completely deaf as though both cochleae had been removed. The condition continued as long as the dog lived.

At this time Munk also concluded that different parts of the auditory cortex function for different sounds. He destroyed parts of the auditory region and then tested the

¹ Studies from the Behavior Research Fund, Chicago: Ernst W. Burgess, Ph.D., acting director. Series B, no. 173.

The writer wishes to acknowledge his indebtedness to Dr. K. S. Lashley.

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animals with the organ (C, c), bass calls, deep noises, whistle (c''', c''''', c'''''''), falsetto calls, and high noises. Ear, head, and body movements were the only criteria that were used to show whether or not the animal reacted to a particular sound. Munk came to the following conclusion: “. . . die hintere Partie der Hörsphäre in der Nähe des Kleinhirns der Wahrnehmung tiefer Töne, die vordere Partie der Hörsphäre in der Nähe der Fossa Sylvii der Wahrnehmung hoher Töne dient” (p. 121).

Luciani and Seppilli ('86) tested Munk's ('81) earlier contention that bilateral destruction of the auditory cortex caused complete and permanent deafness. After three months, the dogs, so affected, reacted to 'Gehörs *empfindungen*,' but not to 'Gehörs *vorstellungen*.' This is contrary to Munk's conclusion.

Kalischer ('07) trained dogs to take food when a certain noise (command) or tone was given and to inhibit the reaction when some other noise or tone (Gegentöne) was given. When both temporal lobes were destroyed in trained animals, they failed to discriminate noises, but were still able to discriminate tones. He concluded that “. . . beide Arten von Hörreaktionen von verschiedenen Bedingungen abhängig waren. . . .” (p. 211). The reaction to tone, according to Kalischer, is infracortical, while to noises (commands, etc.) the reaction is dependent upon the temporal lobe.

Using Kalischer's method of training, Rothmann ('08) reached the same conclusion as Munk, namely, that bilateral destruction of area B B' B results in complete and permanent deafness. If, however, the area is not entirely destroyed, the animals can again learn to react to sounds, but with greater difficulty.

Swift ('10) trained two dogs to discriminate between a food tone c' and a non-food tone e''. After extirpation of the temporal lobes, the dogs still reacted to the food tone c' and inhibited the reaction when e'' was given. He concluded that the “Reaktion auf Töne nach doppelseitiger Schläfenlappenextirpation ein intellektueller Prozess, ein Prozess der

Denkvermögen ist, der aber nicht im Schläfenlappen, sondern in der Rinde extemporal lokalisiert ist'' (p. 688).

Pavlov ('27) reported work on dogs in which conditioned auditory reactions reappear after bilateral extirpation of the acoustic analyzer (temporal region).

After complete removal of the temporal lobes auditory conditioned reflexes still continue to exist . . . and an elementary differentiation can still be effected, while after extirpation of the whole cortex all conditioned reflexes entirely and permanently disappear. Only one conclusion, therefore, can be drawn, namely, that in the cortex, besides the special part of the acoustic analyser, there must still exist some extensions of the analyser dispersed more widely over the cortex, and maybe throughout its whole mass (p. 339).

Such a view is quite in contrast with those offered by previous investigators.

The validity of this earlier work has been severely questioned by Johnson ('13). His dogs, when adequate controls were used, failed to discriminate pitches, but were able to localize noises (buzzer). According to Johnson, the dogs of Kalischer, Swift, and Rothmann were, in all probability, reacting on the basis of secondary cues.

The cyto-architectural structure of the cerebral cortex of a number of rodents, among which the rat was included, has been investigated by Fortuyn ('14). On anatomical grounds, he attempted to localize that part of the cortex which is essential to auditory reactions. Area *p* (fig. 3) is found to correspond to the temporal region—area 20, 21, 22 (Brodmann, '09)—of higher forms. After having determined the differences in breadth and structure of area *p*, particularly layer III, he attempted to grade the animals as to quickness of hearing. They were ranked in the following order: 1) squirrel, 2) guinea-pig, 3) rat, 4) mouse, 5) rabbit, 6) waltzing mouse (totally deaf). No behavior studies were attempted to determine the validity of this order. The animals were ranked according to the writer's estimate, from his observations, as to the quickness of hearing of the animals. He then determined the relation of this measure to the breadth of layer III in area *p*, the number of cochlear wind-

ings, and the number of cochlear nerve fibers. The relationships were not significant. Fortuyn concludes that he could not "... find in area *p*, the auditory cortex (?) of rodents, any variations which could be correlated with function." Thus he is not certain that area *p* is auditory cortex, but believes that this area is homologous to areas 20, 21, and 22 of Brodmann ('09), and he says, "In man area 22 (the first temporal gyrus) certainly has an auditory function" (p. 346).

It is not improbable that Doctor Fortuyn might have found different results if he had made more accurate determinations as to the comparative auditory capacities of the rodents investigated. In recent years psychologists have developed more adequate methods for the study of behavior and cerebral control. Lashley ('22, '26), for instance, has utilized the Yerkes brightness-discrimination box to determine the function of the cerebral cortex in vision, and more recently ('29) he has perfected a method for the study of pattern discrimination. This latter method has opened up possibilities for cerebral study in animals that have hitherto seemed impossible.

In the study of auditory reactions of any animal it is necessary to know the sounds to which that animal is capable of reacting. Hunter ('15, '17), Barber ('15), and Wylie ('19) have shown that rats can be trained to react to auditory stimuli in such a manner that a measure of that reaction can be obtained. Hunter set up differential reactions in the rat for auditory stimuli which are classed as noises, but he failed with tones from tuning forks of 1152 d.v., 1280 d.v., and 4096 d.v., as well as with tones in the lower ranges. He makes the following statement:

The work on auditory sensitivity in the white rat has indicated an insensitivity to tones in the lower portion of the scale and also to some as high as the pitch 4096 d.v. on the fork. It has also demonstrated that the rat can hear noises.

Barber ('15) was able to establish in the rat the habit of localizing a noise (tapping) in from forty to 160 trials, but found that the animal failed to localize pure tones. Wylie ('19) also found that rats would react to noises (buzzer).

PROGRAM OF STUDY

The failure of Johnson, with the dog, and Hunter and Barber, with the rat, to obtain pure-tone discrimination indicated to us that it would be difficult and probably futile to try to establish reactions in the rat to sounds other than those classed as noises. Accordingly, we chose to use stimuli of this latter class and found small electric buzzers satisfactory.

Having decided upon the stimulus, it was necessary to determine some way of training the animal to react to that stimulus. We first tried an apparatus similar to that used by Barber ('15) for localization of sound. She used an octagon-shaped box which was divided into eight sectors, with a stimulus board, which could be tapped upon with a pencil, around the outside of the box. The rats could run freely inside this box. The accuracy of localization was measured in terms of the distance of the point to which the rat came for food from that at which the tapping sound was made. We did not find the procedure very satisfactory, as the animals had a tendency to follow the outside edge of the box rather than to turn and go directly toward the source of the sound.

Next we constructed a Y-shaped maze and attempted to train the animals to go toward the source of the sound, a buzzer sounded in irregular succession at one or the other food box. After training animals for 500 trials without any indications of learning, we changed to the T-shaped apparatus illustrated in figure 1. Again we tried to train the rats to go toward an intermittent sound, but with no greater success than formerly. The process was then reversed and the animals were trained to turn back when the buzzer sounded. This method yielded the desired results and was utilized in the following study. Wylie ('19) also reported that he was unable to train rats to go to the source of a sound, but that they did learn to give a negative reaction to sounds.

PURPOSE OF STUDY

The study was undertaken primarily to determine whether an auditory habit is a function of a part of the cerebral cortex or whether it is a function of the entire cortex. Systematic exploration of the cerebral cortex in trained animals is the only means by which this question can be answered.

Secondly, we wished to effect varying amounts of destruction in the different cortical regions, in order to obtain some knowledge as to the manner of function of the cortical mechanisms utilized in the formation of an auditory habit, and to determine whether or not the quantitative relations reported by Lashley hold good for the auditory mechanisms.

Lashley ('29) has shown that in the maze habit the entire cerebral cortex functions, while for brightness discrimination ('26) only the posterior third of the cerebral cortex is utilized. For the maze Lashley has found a high relationship between the amount of intact cerebral tissue and the performance of the habit, while for brightness discrimination this same relationship exists, but is limited to the tissue within the posterior third of the cerebral cortex and to the amount of postoperative retention. With reference to the latter experiment Lashley makes the following statement:

The physiological work indicates a cerebral area which behaves as a unit whose parts are equivalent in function, capable of summated action and independent of particular cortical association paths (p. 44). . . . in the operative experiments we have really isolated a mechanism which underlies the more complex adaptive reactions: that the mass action shown in these experiments is a general principle of neural activity (p. 44).

EXPERIMENTAL METHOD

The animals in this experiment were trained on the apparatus represented in figure 1. *S* is the starting compartment; *B* and *B'*, the buzzer platforms; *G* and *G'*, the grill plates for punishment; *D* and *D'*, the doors to the food compartments *F* and *F'*; *Bu* and *Bu'*, the buzzers. The buzzer sounded when the rat stepped upon the particular buzzer platform that was adjusted to react. This buzzer adjustment was arranged in

random order, left and right. It follows, then, that if the rat started in the direction of the non-active buzzer, he would proceed through the whole path and obtain food. When he stepped on the platform that sounded the buzzer, he was required to retrace and go to the opposite food box. It may thus be seen that chance responses would allow the rat to obtain food in 50 per cent of the trials without sounding the buzzer.

Suppose we have the following situation: The apparatus is so arranged that the buzzer on the left sounds if the rat steps on the left buzzer platform. When the rat leaves the

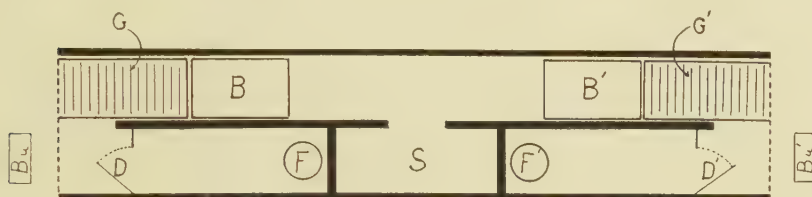


Fig. 1 Apparatus used for training in audition. *S* is the starting compartment; *B*, *B'*, the buzzer platforms; *G*, *G'*, the punishment grills; *D*, *D'*, the doors to the food compartments, *F*, *F'*. *Bu* and *Bu'* are the buzzers. If the animal, started at *S*, steps on *B'* when *D'* is closed, the buzzer *Bu'* sounds; if the animal turns back and goes to *F*, the response is correct. If it crosses to *G'*, the trial is recorded as an error. If the animal passes directly to *F*, the trial is recorded as a chance response.

starting box, he has two alternatives, to go either to the right or to the left. If he goes to the right, it is recorded as a chance response. If, however, he goes to the left, he steps on the buzzer platform which introduces the stimulus. Here again he has two alternatives: he may proceed and be punished on the grill plate, or he may turn around and go to the food compartment located on the right. If he steps on the grill plate, the trial is recorded as an error. If he turns at the sound of the buzzer and goes to the opposite food compartment, it is counted as a correct response. When a rat made eighteen correct responses with no more than two errors within forty trials, we considered that he had learned the problem. Allowing for chance responses, this would corre-

spond to a criterion of eighteen correct responses in twenty trials.

A ten-day rest period was then introduced, following which the rats were again required to reach the original criterion of learning. Immediately after this, they were subjected to cortical operation. An incision was made through the skin, the skull was trephined, and the cortex destroyed by cautery. The lesions varied in locus and extent, covering practically the entire neopallium and involving from 2.6 per cent to 31.7 per cent of the total neopallial cortex.

Ten days after the operation, the rats were returned to the problem and retrained until they again reached the criterion of learning. They were then killed by ether, their brains were removed, fixed in absolute alcohol, and embedded in parlodion for sectioning and staining. The sections were stained with carbothionin and drawings of these were made under a projection lantern. The reconstructions were made according to the method devised by Lashley ('26). With the lesion projected upon his diagram, the locus and extent of the injury were readily determined. The extent was measured with a planimeter.

There are several cues other than auditory to which the animals might conceivably have responded. These, and our methods of eliminating them, are discussed below.

CONTROLS

The apparatus affords no possible differential cues other than the following.

1. Food odors

Food was placed in both food compartments. During each trial one door was closed, leaving a possibility that food odors might differ in the two alleyways. We controlled this possibility by leaving both doors open, and found no effect on the established habit.

2. Ozone from the punishment grills

No current passed through the grills unless the platform was depressed so as to complete the circuit. As a further check the animals were tested when the inductorium was not connected. Their reactions remained unaltered.

3. Directional cues

There was some danger that the experimenter might orient the animal when placing it in the starting box. This was eliminated by orienting the rat sometimes toward the correct alleyway and sometimes away from it.

4. Reactions to secondary auditory cues

The 'setting' of the problem box might have offered cues. This was controlled by 'setting' the apparatus before placing the animal in the starting compartment.

5. Accidental cues from experimenter

Often the experimenter was in another room while the animal was running. During the greater part of the training period the experimenter was engaged in training animals on an entirely different problem, which, accordingly, occupied a great deal of his attention.

EXPERIMENTAL DATA

The complete records for individual animals are given in table 1. This includes the number of trials, errors, and correct responses made by each animal during the learning, the preoperative retention, and the postoperative retention tests. These records do not contain the trials, errors, or correct responses which an animal made during those runs which satisfied the criterion of learning and retention. The percentage of cerebral cortex which was destroyed is given and also an estimate of the amount of disturbance of the internal capsule. The lesions in the internal capsule were rated on a scale of 1 to 3. Thus a rating of 1 means a slight lesion and a rating of 3 means a large lesion. To show the amount of

TABLE 1

Individual learning records for all cases. Initial learning, preoperative and postoperative retention tests. T, trials; E, errors; C, correct responses; Int.Cap., estimate of destruction in the internal capsule. Records for those animals which did not survive the operation are also included

SERIAL NO.	LEARNING			PREOPERATIVE RETENTION			CORTEX DESTROYED, PER CENT	POSTOPERATIVE RETENTION			INT. CAP.
	T	E	C	T	E	C		T	E	C	
1	87	43	3	0	0	0	8.1	0	0	0	0
2	170	63	12	8	1	2	8.2	41	20	12	-
3	100	34	11	0	0	0	8.2	54	11	19	-
4	86	32	4	0	0	0	8.6	16	5	2	0
5	150	53	27	64	7	27	9.2	137	17	52	0
6	80	39	9	0	0	0	10.1	60	6	17	0
7	113	33	28	0	0	0	10.2	20	4	4	-
8	164	57	32	10	2	2	11.0	110	20	36	0
9	200	57	45	0	0	0	11.4	10	1	3	-
10	97	43	12	0	0	0	12.3	71	15	19	0
11	194	65	22	10	2	4	14.3	120	24	44	2
12	130	47	23	0	0	0	16.9	20	5	6	-
13	200	63	51	0	0	0	17.9	66	18	24	2
14	239	76	41	20	3	7	23.6	90	14	34	2
15	254	110	26	3	2	1	26.2	230	81	44	3
16	238	85	28	31	3	12	26.2	67	18	19	0
17	297	121	44	17	8	6	27.6	126	24	44	0
18	240	94	28	0	0	0	31.7	480	192	92	3
19	127	61	4	0	0	0	4.7	28	16	4	0
20	200	102	11	0	0	0	5.1	52	8	23	0
21	296	89	62	0	0	0	5.1	0	0	0	0
22	175	58	30	34	3	17	7.2	30	5	6	0
23	169	70	38	47	8	17	9.8	51	25	6	1
24	250	115	15	0	0	0	10.0	20	3	2	-
25	187	53	47	30	5	13	10.6	28	6	7	0
26	140	50	13	13	3	6	10.6	30	2	14	0
27	100	42	8	0	0	0	10.6	30	8	9	1
28	90	36	12	38	11	12	10.9	10	4	2	0
29	224	76	58	23	3	7	11.4	0	0	0	0
30	120	67	6	0	0	0	12.0	26	8	8	-
31	160	65	10	0	0	0	12.5	40	6	14	0
32	130	45	23	0	0	0	13.8	13	4	2	-
33	168	54	31	0	0	0	15.7	17	2	4	-
34	170	75	24	0	0	0	16.2	7	2	0	-
35	112	44	24	0	0	0	17.2	70	11	21	0
36	236	95	17	50	10	16	26.0	456	125	126	3
37	220	69	42	20	5	4	27.9	79	17	30	0
38	218	76	28	0	0	0	31.7	110	19	40	3

TABLE 1—*Continued*

SERIAL NO.	LEARNING			PREOPERATIVE RETENTION			CORTEX DESTROYED, PER CENT	POSTOPERATIVE RETENTION			INT. CAP.
	T	E	C	T	E	C		T	E	C	
39	230	82	36	0	0	0	8.0	10	1	3	0
40	283	105	44	0	0	0	9.2	0	0	0	0
41	176	62	31	0	0	0	10.0	0	0	0	0
42	220	58	47	10	2	3	12.1	0	0	0	0
43	140	59	19	30	2	15	12.8	0	0	0	0
44	190	100	13	10	1	3	16.1	37	6	14	0
45	104	42	15	0	0	0	17.2	20	1	4	—
46	307	113	39	30	7	10	30.4	18	5	3	1
47	91	38	12	0	0	0	2.7	0	0	0	0
48	169	70	10	10	1	3	4.1	15	2	6	0
49	137	36	25	10	1	1	4.9	20	4	5	0
50	280	70	60	0	0	0					
51	330	96	94	30	6	13					
52	195	81	19	0	0	0					
53	206	67	25	40	4	12					
54	130	55	18	0	0	0					
55	150	61	7	53	5	24					
56	196	64	32	0	0	0					
57	130	52	22	20	4	10					
58	118	36	15	20	6	7					
59	285	105	36	0	0	0					
60	195	60	36	10	2	3					
61	179	85	16	31	10	10					
62	216	86	28	29	12	6					
63	201	100	22	0	0	0					
64	259	94	40	0	0	0					
65	95	38	18	4	1	1					

cerebral tissue destroyed in all of the operated cases we have prepared a composite diagram by superposing the lesions upon one diagram, figure 2. The distribution of the lesions is such that almost all of the neopallium has been investigated.

The protocols, presented in the last part of the paper, show the extent and locus of the lesion in each of the animals. These are also separated according to the regional classification which will be discussed in the next section.

Animals numbered from 1 to 49, inclusive, are those which completed the entire problem. They received the initial training and the preoperative retention tests and survived the operation long enough to regain the initial criterion of learning. Cases 50 to 65, inclusive, are those which did not survive the operation. These were included in the normal records in order to base the learning averages upon as large a number of cases as possible.

A summary of trials, errors, and correct responses—i.e., turning back and going to the opposite food compartment when the buzzer sounds—for learning, preoperative retention,



Fig. 2 Composite diagram showing the amount of cortex explored.

and postoperative retention tests is presented in table 2. N represents the number of cases in each group, M the mean, σ the standard deviation, and P.E._m the probable error of the mean. In the original learning the average for trials is 181.0 ± 5.3 ; for errors, 67.3 ± 2.0 , and for correct responses, 26.6 ± 1.4 . The averages for preoperative retention tests are: trials, 11.6 ± 1.3 ; errors, 2.2 ± 0.3 , and correct responses, 4.3 ± 0.5 ; while for postoperative retention tests the average for trials is 59.9 ± 9.2 ; for errors, 15.6 ± 3.2 , and for correct responses, 16.8 ± 2.3 . The averages for the three criteria of the postoperative retention tests are not as large as the averages of learning. They are, however, consistently higher than those of the preoperative retention tests.

In table 3 are given the differences, for the three criteria, between the means of the postoperative and preoperative retention tests, D ; the probable error of this difference, $P.E._D$; and the ratio of the difference to the probable error of the difference. For all the cases, for trials the ratio of the dif-

TABLE 2

Summary of learning and retention records of all cases. The averages for trials, errors, and correct responses before and after operation are given. The number of cases (N), the means (M), the standard deviation (σ), and the probable error of the mean ($P.E._m$) are given in successive columns

	N	M	σ	P.E. _m
Learning:				
Trials	65	181.0	62.9	5.3
Errors	65	67.3	23.3	2.0
Correct responses	65	26.6	16.6	1.4
Preoperative retention:				
Trials	65	11.6	16.1	1.3
Errors	65	2.2	3.2	0.3
Correct responses	65	4.3	6.3	0.5
Postoperative retention:				
Trials	49	59.9	95.5	9.2
Errors	49	15.6	32.8	3.2
Correct responses	49	16.8	23.9	2.3

TABLE 3

Comparison of preoperative and postoperative retention tests for all cases and for regions p and j . Successive columns show differences (D), probable errors of differences ($P.E._D$), and ratios of differences to probable errors of differences ($\frac{D}{P.E._D}$)

	D	P.E. _D	$\frac{D}{P.E._D}$
All cases:			
Trials	48.3	9.3	5.2
Errors	13.5	3.2	4.3
Correct responses	12.6	2.4	5.3
Area p :			
Trials	83.8	17.3	4.8
Errors	24.2	7.0	3.5
Correct responses	22.0	3.7	6.0
Area j :			
Trials	43.2	14.5	3.0
Errors	11.4	4.0	2.9
Correct responses	11.7	4.2	2.8

ference to the probable error of the difference, $P.E._D$, is 5.2; for errors, 4.3; and for correct responses, 5.3.

Since, when we consider all of the cases together, the difference is well over four times the probable error of the difference in each criterion used, we may conclude that the operations upon the cerebral cortex have resulted in some loss of the habit. The other sections of this table will be discussed in their appropriate context.

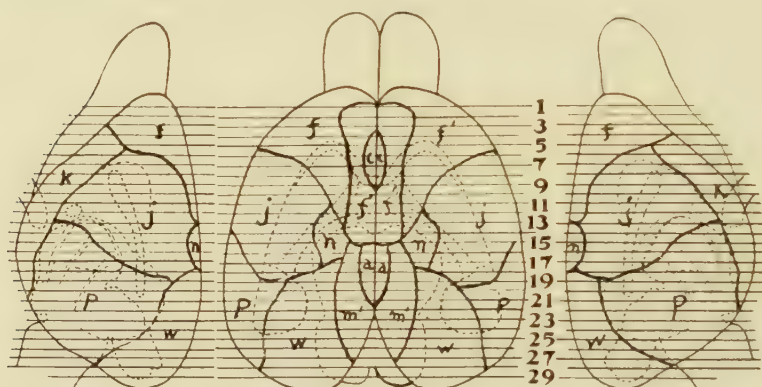


Fig. 3 The chief cyto-architectural areas of the rat's cerebral cortex, modified from Fortuyn ('14) to the proportions of Lashley's diagram.

REGIONAL DIFFERENCES

Next we wish to determine if destruction of any one of the cyto-architectural fields results in greater loss of the habit than the other regions.

The cortex was divided into four regions, according to Lashley's ('29) modification of Fortuyn's areas (fig. 3), as follows:

	<i>Per cent of total cortex</i>
<i>f, f', c, and n,</i>	20.35
<i>j,</i>	27.60
<i>p,</i>	23.40
<i>w, m', and aa,</i>	21.45
<i>k</i> ¹ ,	7.20

¹ Area *k* was involved to so slight an extent that it was not considered.

Since we do not consider area *k*, we have four general cortical fields. The cases were divided according to the region most involved in each. Such a scheme of classification is difficult, as the total lesion may affect one region almost as much as another. For example, of the total lesion, 60 per cent may be in region *j*, the remaining 40 per cent in *p*. By the procedure adopted such a case would be classed as falling in *j*.²

That there is this overlapping from one region to another is shown in the composite diagrams, figures 4, 5, 6, and 7. These figures were obtained by superposing the lesions of a given classification upon one diagram. The lesions in regions *f*, *f'*, *c*, and *n*,³ figure 4, overlap to a slight extent into region *j*, while the lesions in *w*, figure 5, extend into the upper part of region *p* and to a considerable extent into region *j*. The lesions in region *j*, figure 6, overlap regions *p* and *w* and to a lesser degree, region *f*. Similarly, for region *p*, figure 7, the lesions extend into regions *w* and *j* and involve *f* slightly. The involvement of more than one region certainly makes analysis more difficult, but the results seem to justify the procedure.

FIELDS NOT CONCERNED WITH THE AUDITORY HABIT

For each of the regions the number of cases, *N*; the mean, *M*; sigma, *σ*, and the probable error of the mean, *P.E._m*, for each of the three criteria are presented in table 4. For region *w* the average for trials is 10.6 ± 3.0 ; for errors, 1.6 ± 0.05 , and for correct responses, 3.0 ± 0.11 ; for region *f* the average for trials is 11.7; for errors, 2.0, and for correct responses, 3.7. There are only three cases in region *f*, so the *P.E._m* was not calculated. This computation was made for

² This procedure is unsatisfactory, but there is no alternative at present. There is certainly a good bit of individual difference in the distribution of the cyto-architectural fields, and after cortical lesion the limits of the fields involved cannot, of course, be determined by histological methods. At best, we can therefore only guess at the extent of the different fields and deal with the data so as to allow for a rather wide range of variation.

³ The regions shall be called *f*, *j*, *p*, and *w* for convenience.

region *w*, although there are only eight cases. For the sake of comparison the averages for preoperative retention tests, table 2, are again given. They are for trials, 11.6 ± 1.3 ;

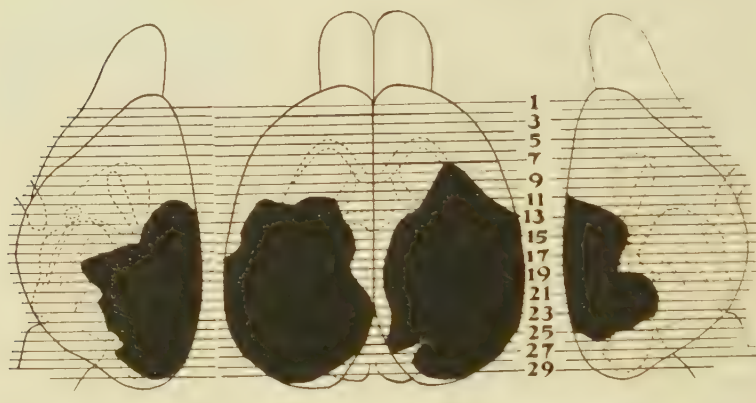
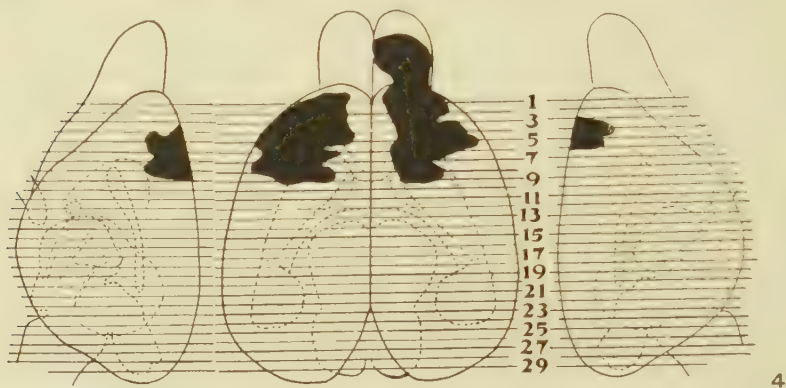


Fig. 4 Total extent of lesion involving area *f*, with some overlapping of area *j*. The olfactory bulbs were injured in one animal.

Fig. 5 Total extent of lesions involving chiefly area *w*, with overlapping of areas *p* and *j*.

for errors, 2.2 ± 0.3 , and for correct responses, 4.3 ± 0.5 . The averages of the data for postoperative retention tests for the cases in region *w* and *f* are not significantly different from those of the preoperative retention tests.

FIELDS SHOWING RELATION TO AUDITORY HABIT

Those cases falling in regions *j* and *p* present a different picture. The averages for region *j* are: trials, 54.9 ± 14.5 ; for errors, 13.6 ± 4.0 , and for correct responses, 15.9 ± 4.1 ;

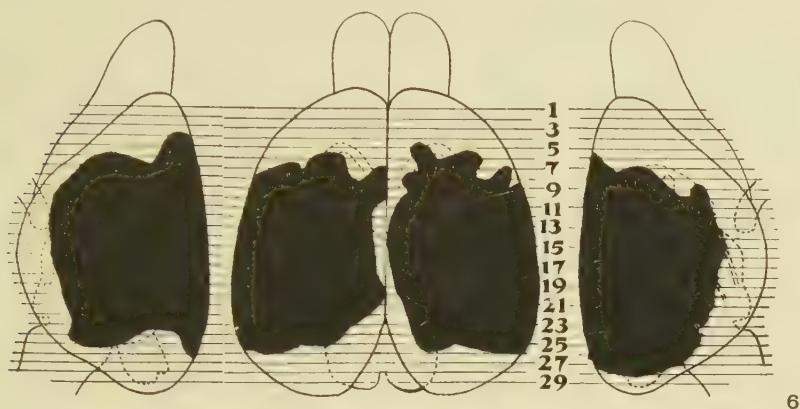


Fig. 6 Total extent of lesions involving chiefly area *j*, with overlapping of areas *w*, *p*, and *f*.

Fig. 7 Total extent of lesions involving chiefly area *p*, with overlapping of area *w*, *j*, and *k*.

while for region *p* the average number of trials is 95.4 ± 17.3 ; errors, 26.4 ± 7.0 , and correct responses, 26.2 ± 3.6 . Comparing these results with the preoperative retention-test averages, which are presented above, we note that they are conspicuously higher according to all three criteria. It seems

clear that those animals which show loss of the habit are the ones in which regions j and p are affected.

Returning to table 3, we may consider the comparison of postoperative and preoperative retention tests for regions j and p . The differences for region p are: trials, 83.8; errors, 24.2, and correct responses, 22.0. For region j they are: trials, 43.2; errors, 11.4, and correct responses, 11.7. The difference divided by the probable error of the difference for

TABLE 4

Comparison of the average postoperative retention records for the cortical regions, p , j , w , and f . The columns contain the number of cases in each region (N), the mean (M), the standard deviation (σ), and the probable error of the mean ($P.E._m$)

	N	M	σ	P.E. _m
Area p :				
Trials	18	95.4	108.5	17.3
Errors	18	26.4	43.7	7.0
Correct responses	18	26.2	22.7	3.6
Area j :				
Trials	20	54.9	95.9	14.5
Errors	20	13.6	26.4	4.0
Correct responses	20	15.9	27.4	4.1
Area w :				
Trials	8	10.6	12.7	3.0
Errors	8	1.6	2.3	0.1
Correct responses	8	3.0	4.7	0.1
Area f :				
Trials	3	11.7		
Errors	3	2.0		
Correct responses	3	3.7		

region p for trials is 4.8; for errors, 3.5, and for correct responses, 6.0, while for region j these same ratios are: trials, 3.0; errors, 2.9, and correct responses, 2.8.

ANALYSIS OF DISTURBANCES AFTER LESION IN FIELD j

Since the differences for region p are much larger and statistically more reliable than those for region j , it is necessary to see whether the loss in region j is due to the cortical destruction or to some other factors not yet accounted for. There are three possible reasons for our results which need consideration.

1. The loss may be due to those cases classed in region j that overlap region p . Table 5 is a summary of these cases. For the cases in which region p as well as j is injured the averages are: for trials, 88.8 ± 26.9 ; for errors, 22.1 ± 7.3 , and correct responses, 25.7 ± 7.7 . Referring to table 3, we see that these results are approximately the same as those in which region p is involved more than any other region. It is clear that a part of the high average for region j is due to overlapping with region p .

TABLE 5

Records of those cases classified in region j which overlap region p . Serial no., trials (T), errors (E), correct responses (C), and percentage of cortex destroyed by the lesion (L) are given in successive columns. The averages for trials, errors, and correct responses and percentage of cortex destroyed are given at the bottoms of the corresponding columns, also the probable errors of the averages

SERIAL NO.	T	E	C	L
23	51	25	6	9.8
25	28	6	7	10.6
27	30	8	9	10.6
31	40	6	14	12.5
33	17	2	4	15.7
34	7	2	0	16.2
35	70	11	21	17.2
36	456	125	126	26.0
37	79	17	30	27.9
38	110	19	40	31.7
Averages	88.8	22.1	25.7	17.8
P.E. _{av.}	26.9	7.3	7.7	

Referring to those cases in area j in which area p is not involved, table 6, our average for trials is 20.9 ± 3.2 ; for errors, 5.0 ± 0.96 , and for correct responses, 6.1 ± 1.5 . From table 2 we know that the average for preoperative retention tests for trials is 11.6 ± 1.3 ; for errors, 2.2 ± 0.3 , and for correct responses, 4.3 ± 0.5 . The effects from the lesions in j , where p is not disturbed, are only slightly higher than the postoperative retention tests.

It seems quite evident that those cases in region j which do not overlap with region p show very little loss of the habit.

2. The loss where p does not seem to be involved directly may be due to interruption of fiber tracts to p . The fiber tracts to area p are contained in the internal capsule, which swings laterally from the thalamus to enter the external capsule at approximately level 16, figure 2. Most of the lesions produce some effect upon the underlying white substance of the brain. Thus the fibers in the external capsule to area p would be affected in these cases. Further, the posterior margin of area j is directly over the fibers which swing

TABLE 6

Records of those cases classified in region j which do not overlap region p . Serial no., trials (T), errors (E), correct responses (C), and percentage of cortex destroyed (L) are given in successive columns. The averages for trials, errors, correct responses, and percentage of cortex destroyed are given at the bottoms of the corresponding columns, also the probable errors of the averages

SERIAL NO.	T	E	C	L
19	28	16	4	4.7
20	52	8	23	5.1
21	0	0	0	5.1
22	30	5	6	7.2
24	20	3	2	10.0
26	30	2	14	10.6
28	10	4	2	10.9
29	0	0	0	11.4
30	26	8	8	12.0
32	13	4	2	13.8
Averages	20.9	5.0	6.1	9.1
P.E. _{av.}	3.2	1.0	1.5	

posteriorly from the internal capsule to supply area p . Interruption of these fibers at this level would probably have the same effect as removing the cortex in area p . All those cases in area j were selected in which the lesion was so located that the fibers to area p from the thalamus might be affected and they were contrasted with the cases which did not affect this critical region.

Tables 7 and 8 give these data. Table 7 contains those cases classed in area j in which the lesion does, or may, interrupt the radiations to area p . The last column gives an esti-

mate of the extent of involvement of the internal capsule. Table 8 contains those cases in area *j* which cannot possibly affect the radiations to area *p*. The groups are comparable with respect to total extent of lesion, so that any difference which exists must be due to interruption of fibers or locus of

TABLE 7

Cases with lesions in regions j which may or do affect the radiations to region p. Serial no., trials (T), errors (E), correct responses (C), percentage of cortex destroyed (L), and estimate of disturbance of the internal capsule (Int.Cap.) are given in successive columns. The average lesion and the averages and probable errors of the averages for trials, errors, and correct responses are given at the bottoms of the columns

SERIAL NO.	T	E	C	L	INT.CAP.
23	51	25	6	9.8	1
25	28	6	7	10.6	0
27	30	8	9	10.6	1
29	0	0	0	11.4	0
34	7	2	0	16.2	0
35	70	11	21	17.2	0
36	456	125	126	26.0	3
38	110	19	40	31.7	3
Averages	94.0	24.8	26.1	16.7	
P.E. _{av.}	33.4	9.3	9.5		

TABLE 8

Cases with lesions in region j which do not affect the radiations of region p. Serial no., trials (T), errors (E), correct responses (C), percentage of cortex destroyed (L), and estimate of disturbance of the internal capsule (Int.Cap.) are given. The average for each is given at the bottom of the column

SERIAL NO.	T	E	C	L	INT.CAP.
19	28	16	4	4.7	0
20	52	8	23	5.1	0
21	0	0	0	5.1	0
22	30	5	6	7.2	0
24	20	3	2	10.0	0
26	30	2	14	10.6	0
28	10	4	2	10.9	0
30	26	8	8	12.0	—
31	40	6	14	12.5	0
32	13	4	2	13.8	—
33	17	2	4	15.7	—
37	79	17	30	27.9	0
Averages	28.8	6.3	9.1	11.3	
P.E. _{av.}	3.9	1.0	1.8		

cortical lesion. There is a great difference between the two groups when we examine the averages for the three criteria. The lesions that affect the thalamic radiations show nearly as great a loss as those that occur in area *p* itself (compare table 3). The cases in which the thalamic radiations to area *p* are not cut approximate the preoperative retention tests as shown in table 2.

It is fairly certain, therefore, that the loss of the habit for those cases that are classed in area *j* is not due to the fact that the cortex in area *j* is destroyed, but rather to the partial destruction of area *p* or to the interruption of the fibers leading to area *p*.

3. Part of region *j* may actually be concerned in audition. It is not possible to say whether the cortex in this region, which is directly over the fibers from the internal capsule, is or is not functional in the auditory habit. To determine this, the cortical region overlying the auditory radiations would have to be destroyed without permitting the operation to affect the underlying structures. It would be difficult, although not impossible, to accomplish this, as the cerebral cortex of the rat's brain is relatively thin. As we have stated elsewhere, most of the lesions do effect some disturbance of the underlying white substance, so our data do not permit adequate analysis of this question. If this region is functional in audition, then the cephalad boundary of region *p* would have to be shifted so as to include part of region *j*. However, the limits of region *p* would not be increased to a very large extent. On the other hand, the transitional region between regions *j* and *p* may not be sharply differentiated from a functional point of view.

The data show that destruction of regions *f*, *w*, or *j* has no effect on the retention of the auditory habit investigated, whereas the destruction of the posterolateral part of the cortex results in the loss of the habit. Fortuyn's area *p* delimits this region fairly closely.

RELATION OF THE FUNCTION TO EXTENT OF LESION

The correlations between the extent of the total lesion and the loss of the habit for areas *p* and *j* for each of the three criteria are presented in table 9. The average and total range of lesion are also given for each of the four regions. These figures are comparable for regions *j*, *p*, and *w*, but region *f* contains only three cases and the lesions within this group are small. The correlations were obtained from the division of the cases as they are given in table 1. For regions *w* and *f*

TABLE 9

Percentages of cortex destroyed and correlations between trials, errors, and correct responses and percentage of cortex destroyed in regions p and j

GROUPS	CORRELATIONS	LESION	
		Average extent	Range
Postoperative retention (all cases)		13.8	2.7-31.7
Area <i>p</i> :		15.7	8.1-31.7
Trials	.63 ± .10		
Errors	.61 ± .11		
Correct responses	.59 ± .11		
Area <i>j</i> :		13.4	4.7-31.7
Trials	.30 ± .14		
Errors	.29 ± .15		
Correct responses	.38 ± .14		
Area <i>w</i>		14.5	8.0-30.4
Area <i>f</i>		3.9	2.7- 4.9

the correlations were not computed, since the loss due to the operation in these two regions did not exceed the average loss due to the time factor alone, as measured by the preoperative retention tests.

The Spearman rank-order method of computing correlations was used.⁴ The results for area *p* are: trials, $0.63 \pm .10$; for errors, $0.61 \pm .11$, and for correct responses, $0.59 \pm .11$. In area *j* they are: for trials, $0.30 \pm .14$; for errors, $0.29 \pm .15$, and for correct responses, $0.38 \pm .14$. We have shown that the loss found in area *j* is not caused by the lesion in *j*, but due rather to the fact that area *p* is partially destroyed

⁴ P.E. $\rho = 0.7063 \frac{1 - \rho^2}{N}$. (Kelley, T., Statistical Method, N. Y., 1924.)

or that the thalamic radiations to area *p* are affected. The small relationship is probably due to the fact that the larger the lesion in area *j*, the greater the involvement of area *p*.

A correlation of 0.63 is not usually considered to indicate a very high degree of relationship. On the other hand, the correlation can hardly be expected to express the true relationship, since several other factors operate to obscure the picture. The larger lesions are not confined to area *p* alone, but may extend into other regions. Further, the subcortical disturbances are unaccounted for in the correlations. On the whole, there is a tendency for the larger lesions to show greater subcortical destructions. It is noteworthy that this correlation is about the same as those found by Lashley in totally different problems. Lashley ('26) found a correlation of 0.72 ± 0.05 between postoperative retention of the habit of brightness discrimination and the extent of the lesion in the occipital third of the cerebral cortex. For the maze the same investigator ('29) found that the relationship between postoperative retention tests and the extent of the lesion, irrespective of the locus of the injury, was 0.59 ± 0.06 for errors and 0.60 ± 0.06 for trials. The fact that these results, from one field of investigation to another, are relatively the same size tends to make them more significant. It seems clear that the degree of retention of an auditory habit is closely related to the amount of the tissue remaining intact in area *p*.

CONCLUSIONS

From the results presented in the preceding pages it is evident that the posterolateral part of the cerebral cortex functions in the particular auditory habit established. Fortuyn's area *p*, which he considers homologous to Brodmann's area 20, 21, and 22, delimits this region with a high degree of accuracy.

Just as Lashley ('26) found that destruction in field *w* abolished the habit of brightness discrimination in the rat, we have found that large destruction of area *p* may abolish an auditory habit. Moreover, we found, as Lashley found for

the visual habit, that the loss of this region after formation of the habit does not preclude the possibility of the reformation of the habit. It is possible that the cerebral cortex outside of area *p* may assume this function. Pavlov ('27) believes that the temporal region of the dog's brain is the acoustic analyzer, but that other cortical regions, and probably all of the cortical tissue, receive auditory impulses. If such is the case, then the remaining cortical tissue may carry out the auditory functions (p. 339). It is just as possible that the subcortical centers can carry out this simple function. Herrick ('26), in his discussion of Lashley's work on the function of the cortex in the habit of brightness discrimination, is inclined to believe that the habit, after loss of the cortex, is thalamic rather than due to a vicarious functioning of the cortical tissue. Our evidence shows only that if the cortex in area *p* is present, it plays a part in the formation and retention of the auditory habit.

Area *p* seems to be a region for the reception and transmission of those auditory impulses to which the rat is capable of responding. Also, this region seems to act as a facilitating mechanism in the formation of the habit, as is suggested from the fact that two animals, nos. 18 and 36, with large destructions in area *p*, required more trials to relearn the habit after the operation than any animal required to learn it originally. Lashley ('26) found that none of the animals in which the visual cortex was destroyed required more trials to relearn the habit of brightness discrimination than any normal animal required in learning. This difference suggests that the subcortical auditory mechanisms are, for the functions studied, more dependent upon the cortex than are the subcortical mechanisms which function in brightness discrimination. For pattern vision, on the contrary, Lashley has found that the cortical mechanisms are absolutely essential. It seems possible, therefore, that the subcortical mechanisms are more dependent on the cortex in some habits than in others.

The correlations found show a relationship between the amount of tissue destroyed and the ability to relearn the

habit when the destruction of the tissue occurs in or near area *p*. The highest correlation between the extent of the injury and any measure of postoperative retention is 0.63. This suggests the same kind of mass relationship for an auditory habit that Lashley ('26) found in the visual cortex of the rat for the habit of brightness discrimination.

The results of the investigation raise several questions.

1. What will be the effect on the formation of auditory habits if the auditory cortex is removed before training? Lashley ('26) found that rats with removal of the visual cortex previous to training learned as well as normal rats.

2. Since removal of the auditory cortex affects a simple auditory habit, what will be the effect of such lesions on other types of auditory reactions, such as localization of sound, intensity differences, etc.?

3. The problem of pure-tone discrimination also needs further investigation. Lashley's revolutionary method for visual-pattern discrimination in rats suggests that tone discrimination may be possible in rats if an adequate technique is discovered.

SUMMARY

1. The cerebral cortex of the rat plays a part in the formation of a simple auditory habit.

2. The function is not determined by the entire cortex, but is limited to the posterolateral part of the cerebrum.

3. The region involved in audition is closely delimited by Fortuyn's area *p*.

4. Large destruction in the auditory region seems to cause complete loss of the habit, but the habit can be reacquired.

5. The data show that there is a relationship between the extent of the destruction and the degree of postoperative amnesia.

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PLATES 1 TO 5

EXPLANATION OF FIGURES

Diagrams of the lesions in the series of cases trained in the auditory habit, arranged according to regional classification. For each diagram the figure to the left is the identification number of the cases used in the tables and text; that to the right, the percentage of the cortex destroyed.

